

UDC 591.524.11(282.257.6.05)

MACROZOOBENTHOS OF THE SUSUYA RIVER ESTUARY (SAKHALIN ISLAND): II. BOTTOM COMMUNITIES AND DISTRIBUTION OF KEY SPECIES

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Received 09.10.2023; revised 28.04.2024;
accepted 12.08.2025.

Communities of macrozoobenthos and their characteristics in river estuaries of Sakhalin Island have not been studied properly. The composition of bottom communities in most estuaries of short rivers on the island is very limited in contrast with that of estuaries of other rivers in the Russian Far East. The Susuya River estuary – a full-sized one compared to estuaries of small rivers of the island – was surveyed in September 2022. The aim of the work is to describe major patterns of distribution of bottom communities, their structure, key species, and trophic characteristics of macrozoobenthos along the salinity gradient in the full-size Susuya River estuary on Sakhalin Island. Bottom communities of the estuary were identified by cluster and ordination analysis. The main communities, trophic characteristics, and distribution features of key macrozoobenthic species along the Susuya River estuary are described. Data on major patterns of distribution of macrozoobenthic communities, key species, and trophic groupings in the Susuya River estuary are provided. In total, 11 communities of macrozoobenthos were identified and united into five types: a community of the riffle separating the estuary from above, communities of the δ -chorohaline zone, communities of the middle estuary oligohaline zone, communities of the lower estuary polyhaline–mesohaline zone, and a community of the river mouth. The community of the water's edge is confined to the river mouth and to the polyhaline–mesohaline zone. The main communities of the estuary are *Corbicula japonica*, *Macoma balthica*, and *Fluviocingula nipponica* + *Macoma balthica*. Environmental factors most affecting the distribution of key macrozoobenthic species are the water salinity and, to a lesser extent, the depth. The type of sediment is not a determining factor.

Keywords: estuary, macrozoobenthos, bottom community, trophic characteristics, Sakhalin Island

Estuaries are zones, where river freshwater mixes with seawater; there, polyhaline, mesohaline (brackish), and oligohaline (freshened) parts are allocated [Aladin, 1988; Aladin, Plotnikov, 2013; Khlebovich, 1974, 1989]. Features of hydrological characteristics of estuaries determine shifts in key macrobenthos species and the development of unique bottom communities there. Ultrafast sedimentation of suspended and dissolved mineral and organic matter in the zone of the effect of the 'marginal filter' results in frequent changes in the trophic groups of benthos within the limited area of the estuary [Lisitsyn, 1994]. For the same reason, estuary ecosystems are characterized by increased productivity [Kolpakov, 2018; Saf'yanov, 1987].

Communities of macrozoobenthos and their characteristics in river estuaries of Sakhalin Island have not been sufficiently studied [Labay et al., 2022; Watercourses of Sakhalin Island, 2015]. In the most properly analyzed estuary, that of the Manuy River, typical of major short rivers on the island, the composition of benthic communities is very limited compared to that of estuaries of other rivers in the Russian Far East [Labay et al., 2022].

In September 2022, the Susuya River estuary, full-sized in comparison with estuaries of short rivers on the island, was surveyed. The material of the study formed the basis of this work.

The aim of the work is to describe the main patterns of distribution of benthic communities, their structure, key species, and trophic characteristics of macrozoobenthos along the salinity gradient in the full-sized estuary of the Susuya River on Sakhalin Island.

MATERIAL AND METHODS

The methods for macrozoobenthos sampling and processing have been described by us earlier, as well as the volume of collected data [Labay et al., 2024].

For the identification of benthic communities and ordination constructions, we used the Q index ($\text{cal} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) reflecting species abundance. It is equivalent to the energy expenditure of all individuals of the i -th species on respiration [Vilenkin, Vilenkina, 1979]:

$$Q = k \cdot B_i^{0.75} \cdot N_i^{0.25},$$

where B_i ($\text{g} \cdot \text{m}^{-2}$) and N_i ($\text{ind.} \cdot \text{m}^{-2}$) are the specific biomass and density of the i -th species *per* 1 m^2 , respectively.

The k coefficient is taken to be 0.178 for Polychaeta; 0.115 for Oligochaeta; 0.126 for Gastropoda; 0.089 for Bivalvia; 0.302 for Amphipoda; 0.133 for Cumacea, Isopoda, Mysida, and Decapoda; 0.189 for Diptera; and 0.115 for Agnatha [Alimov et al., 2013; Golubkov, 2000].

Clustering of benthic stations when describing communities of benthic hydrobionts was carried out according to the similarity index introduced by J. Czekanowski [Czekanowski, 1909; Sørensen, 1948]:

$$C_{1,2} = 2 \sum (MIN_{x_{1i}, x_{2i}}) / (\sum x_{1i} + \sum x_{2i}),$$

where x_{1i} and x_{2i} are abundance values of the i -th species (Q) at conditional stations 1 and 2, respectively.

Benthic stations were united into a community if the index value exceeded 40%. This value corresponds to the condition that the biomass or Q of the dominant species is at least 10% of the total one, with an occurrence frequency of 100%. Clustering of the original matrices was performed by the unweighted pair group method with arithmetic mean [Duran, Odell, 1977].

To describe bottom communities, the following parameters were used: number of species (S); specific abundance (density) (N , $\text{ind.} \cdot \text{m}^{-2}$); biomass (B , $\text{g} \cdot \text{m}^{-2}$); relative species abundance (N , % of total macrozoobenthic abundance); relative species biomass (B , % of total macrozoobenthic biomass); and frequency of occurrence (FO , %). The community structure was analyzed using the density index [Brot-skaya, Zenkevich, 1939] or the relativity coefficient [Kuznetsov, 1963]:

$$RC = B \cdot FO,$$

where B is the relative biomass (%) or Q (%);

FO is the frequency of occurrence (%).

When structuring communities, we took into account the proportion of each species (form) in the mean total macrozoobenthic biomass, FO, and RC. A species was considered dominant if the RC value was in the range of 1,000–10,000. Bottom communities are named according to their dominant species.

The main patterns of benthic distribution are described using ordination graphs constructed by the principal component analysis [Kalinina, Soloviev, 2003] with the Statistica software (v. 8).

For comparative procedures, the Shannon diversity index (entropy index) (I , bit-species⁻¹) was used [Shannon, 1948; Shannon, Weaver, 1949], separately for density (I_N) and biomass (I_B). Also, the ABC method (abundance/biomass comparison method) [Warwick, 1986] by the ABC index [Meire, Dereu, 1990] was applied.

The feeding type of individual macrozoobenthic species was determined based on literature data [Izvekova, 1980; Kanaya et al., 2008; Konstantinov, 1959; Macdonald et al., 2010; Nielsen et al., 1995; Riisgård, 1991; Toba, Sato, 2013; Vedel, Riisgård, 1993]. The following nomenclature was used for the feeding type: Br, browser; De, deposit feeder; Dt, detritus feeder; Gr, grazer; Pr, predator; Sc, scavenger; Sp, suctorial parasite; and Su, suspension feeder (filter feeder). Some species feature a combination of several feeding types, and this is reflected in a mixed characteristic, for example Dt, Br, Sc, or Dt, Su, or De, Su.

RESULTS AND DISCUSSION

The key communities. According to the dendrogram of the similarity of benthic stations, 8 clusters were identified (provided that sta. 34 was combined with cluster 29–14), and also 3 separate stations comparable with bottom communities (Fig. 1).

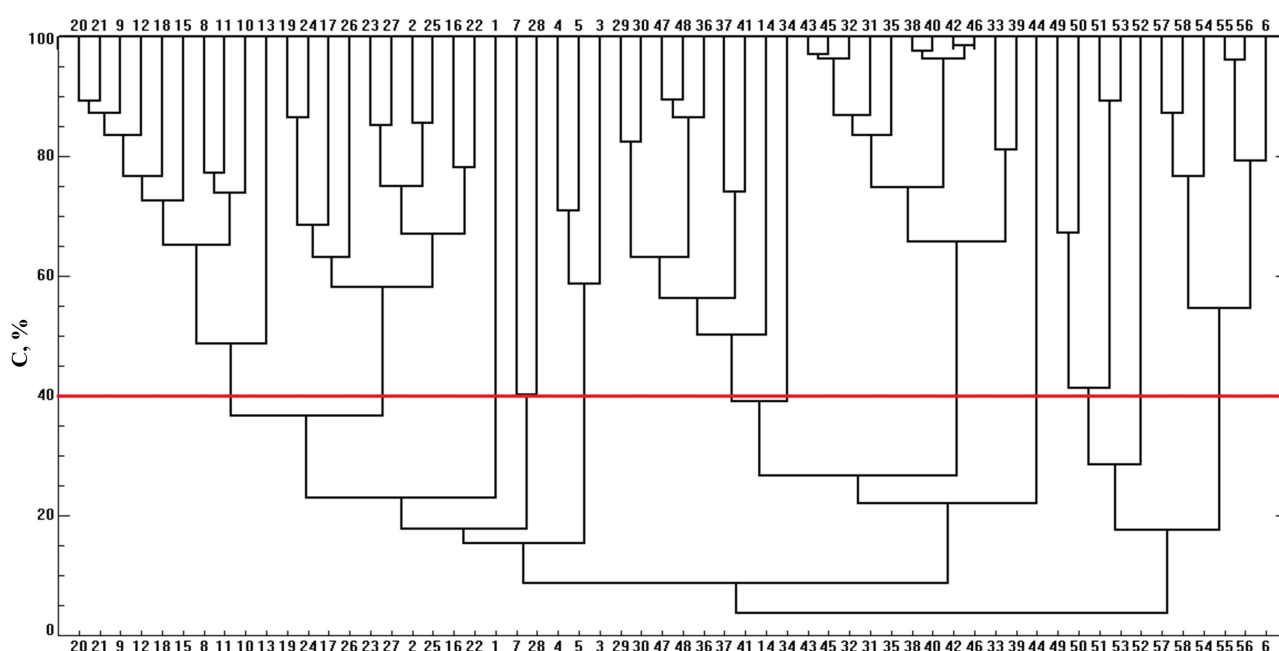


Fig. 1. Dendrogram of the similarity for macrozoobenthos sampled at various stations

Cluster 4, 5, 3, (6) identifies a benthic community dominated by the brush-clawed shore crab *Hemigrapsus takanoi* Asakura & Watanabe, 2005 (74.5% of the total biomass). Subdominants in this community are a gastropod *Fluviocingula nipponica* Kuroda & Habe, 1954 and a bivalve *Macoma balthica* (Linnaeus, 1758) (together, 10.4% of the total biomass). The community is localized in the polyhaline estuary zone (Table 1, Fig. 2). The second cluster, 20, 21, 9, 12, 18, 15, 8, 11, 10, 13, corresponds to the lower estuary polyhaline–mesohaline zone; it is identified as the *Fluviocingula nipponica* + *Macoma balthica* community (predominant species account for 79.5% of the total biomass). Subdominants are polychaetes *Hediste japonica* (Izuka, 1908) and Capitellidae indet. (together, 4.7% of the total biomass). The community is confined to coastal *Zostera* thickets, which is a substrate for a gastropod *F. nipponica*. Both communities are coastal rather than estuarine ones, as their predominant species are common in coastal shallows of Southern Sakhalin [Golikov et al., 1985].

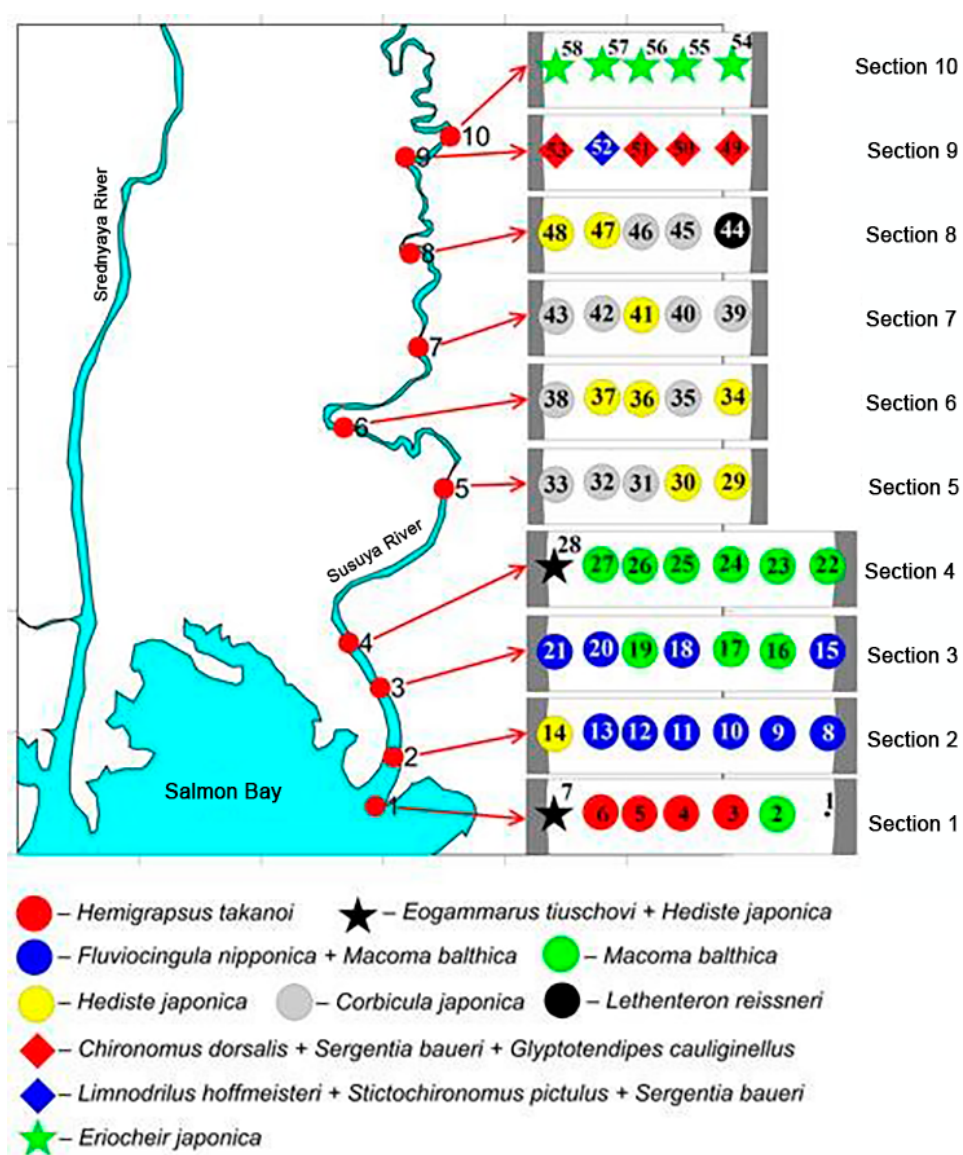


Fig. 2. Location of the major macrobenthic communities in the Susuya River estuary

Table 1. Indicators of macrobenthic abundance in bottom communities of the Susuya River estuary

Parameter		Community (by the dominant species)										
		—	<i>Eogammarus tiuschovi</i> + <i>Hediste japonica</i>	<i>Hemigrapsus takanoi</i>	<i>Fluviocingula nipponica</i> + <i>Macoma balthica</i>	<i>Macoma balthica</i>	<i>Hediste japonica</i>	<i>Corbicula japonica</i>	<i>Lethenteron reissneri</i>	<i>Chironomus dorsalis</i> + <i>Sergentia baueri</i> + <i>Glyptotendipes cauliginellus</i>	<i>Limnodrilus hoffmeisteri</i> + <i>Stictochironomus pictulus</i> + <i>Sergentia baueri</i>	<i>Eriocheir japonica</i>
Station numbers		1	7, 28	4, 5, 3, 6	20, 21, 9, 12, 18, 15, 8, 11, 10, 13	19, 24, 17, 26, 23, 27, 2, 25, 16, 22	29, 30, 47, 48, 36, 37, 41, 14, 34	43, 45, 32, 31, 35, 38, 40, 42, 46, 33, 39	44	49, 50, 51, 53	52	57, 58, 54, 55, 56
Depth, m		0.12	0.15–0.4	0.25–0.75	0.1–2	0.5–2.1	0.15–2	0.25–1.8	0.2	0.3–1.6	1.3	0.08–0.15
Sediment type		fine sand, black and grey silt	from siltstone to pebbles with sand	fine sand mixed with siltstone and pebbles	black mud, often mixed with siltstone and fine sand	black silt	black mud, siltstone, sand, clay, pebbles	coarse sand, pebbles, silt	black silt	siltstone, detritus	siltstone, detritus	pebbles, gravel, sand
Salinity, psu		15.2	15.2–24.8	15.2–22.3	18.1–21.7	21.7–25	3.8–11.7	0.6–11.7	0.6	0.1	0.1	0.1
Biotope		mouth	mouth, lower estuary zone (water's edge)	mouth	lower estuary zone	lower estuary zone	middle estuary zone	middle estuary zone	upper estuary zone	upper estuary zone	upper estuary zone	upper estuary zone, riffle
Number of species (S)		12	19	27	27	27	23	24	11	12	7	20
Specific abundance (N), ind.·m ⁻²		350	1,870 ± 243	419 ± 57	5,745 ± 776	2,134 ± 297	1,253 ± 163	1,206 ± 134	1,787	2,940 ± 334	2,040	3,529 ± 336
Biomass (B), g·m ⁻²		0.145	3.27 ± 0.42	6.25 ± 0.98	41.9 ± 4.88	35.1 ± 4.41	17.0 ± 2.69	357 ± 62.6	149.6	3.08 ± 0.293	1.051	23.4 ± 2.78
Biomass (B) of the dominant, %		—	58.4	74.5	79.5	88.4	24.8	98.7	88.4	86.2	77.5	91.7
Biomass (B) of separate groups, %	Ol	0	0.1	0	0.1	0.5	0.02	0.03	0.6	6.0	37.7	4.6
	Po	16.3	25.4	1.8	5.0	2.6	26.2	0.8	9.4	0.5	7.4	1.0
	Ga	23.3	7.6	11.4	59.6	7.5	11.4	0.3	0	0	0	0
	Bi	28.5	0.2	5.5	25.8	88.8	37.7	98.7	0	0	0	0.002
	Am	9.8	44.9	2.2	1.4	0.3	0.4	0.02	0	0	0	0.4
	Is	2.1	5.5	0.7	0.4	0.04	0.9	0.04	0	0	0	0.003
	My	0	1.9	0.01	0.5	0.01	0.3	0.002	0	0.6	0	0.02
	De	0	13.8	78.3	7.2	0.1	22.4	0.2	1.0	0	0	91.7
	Di	0	0.1	0	0.003	0.01	0.1	0.01	0.6	93.0	54.9	2.3
Ag	0	0	0	0.0	0.0	0	0	88.4	0	0	0	
<i>I</i> , bit·species ⁻¹	<i>I_N</i>	0.64	1.72	2.20	1.75	1.91	1.86	1.92	1.32	1.40	1.46	1.35
	<i>I_B</i>	2.15	1.87	1.12	1.47	0.57	1.65	0.09	0.45	1.40	1.59	0.40
<i>I_{ABC}</i> , %		17.9	5.8	33.2	14.6	22.6	13.5	19.0	31.2	15.4	7.7	11.8

Note: Ol, Oligochaeta; Po, Polychaeta; Ga, Gastropoda; Bi, Bivalvia; Am, Amphipoda; Is, Isopoda; My, Mysida; De, Decapoda; Di, Diptera; Ag, Agnatha.

Transect 4 in the lower estuary zone, completely filled with mesohaline waters, is occupied by the *Macoma balthica* community identified by cluster 19, 24, 17, 26, 23, 27, 2, 25, 16, 22 (see Fig. 2). This community partially penetrates transect 3 and is also recorded in the littoral of the mouth transect. The dominant species accounts for 84.4% of the total biomass. Another 5.5% cover subdominants: a gastropod *F. nipponica* and a polychaete *H. japonica*. The described community is typical of brackish-water and marine lagoons of Sakhalin Island; sometimes, it is noted on the sea coast [Golikov et al., 1985; Kafanov et al., 2003; Labay, 2009; Labay et al., 2016]. In river estuaries on the island, it was recorded for the first time.

The *Eogammarus tiuschovi* (Derzhavin, 1927) + *Hediste japonica* community was registered at littoral sta. 7 and 28 in the mouth and in the lower estuary zone (Fig. 2). With the proportion of dominant species of 58.4% of the total biomass, it is characterized by a long list of subdominants (6 species; 38.3% of the total biomass). Those are a shrimp *Crangon amurensis* Bražnikov, 1907; an isopod *Gnori-mosphaeroma ovatum* (Gurjanova, 1933); an amphipod *Ampithoe lacertosa* Spence Bate, 1858; a mysid *Neomysis awatschensis* (Brandt, 1851); polychaetes Capitellidae indet.; and a gastropod *Assimineia lutea* A. Adams, 1861. At sta. 1, also included in a supercluster of stations covering the mouth and lower estuary zone, there were no dominant species.

Only two bottom communities were localized on transects 5–8 of the middle estuary zone (see Fig. 2). The first one was identified by cluster 29, 30, 47, 48, 36, 37, 41, 14, 34. The community was dominated by a polychaete *H. japonica* (24.8%). A close community with the prevalence of the same species is typical of estuaries on Sakhalin Island [Labay et al., 2022; Watercourses of Sakhalin Island, 2015], but in the Susuya River estuary, the described community is completely different in structure. There, the list of subdominants covers a bivalve *Corbicula japonica* Prime, 1864; a crab *Deiratonotus cristatum* (De Man, 1895); and a gastropod *As. lutea* (together, 65.8% of the total biomass). This community is noted in the entire range of surveyed depths, from the littoral to the waterway, chiefly on fine sand and silt. The driver of its distribution is the water salinity, which is in the range between α - and δ -chorohaline boundaries. The second community is associated with cluster 43, 45, 32, 31, 35, 38, 40, 42, 46, 33, 39; it is characterized by the dominance of a bivalve *C. japonica* (98.7% of the total biomass) and the lack of subdominants. It is localized in a depth range of 0.25–1.8 m, mostly on coarse sand with pebbles and silt. This community is typical of oligohaline areas of lagoons and lagoon lakes of Sakhalin Island, Japan, and Primorye, where it occurs at the optimum water salinity of 1.2–2.5 psu [Baba et al., 1999; Kafanov et al., 2003; Reservoirs of Sakhalin Island, 2014; Water Biota of Tunaicha Lake, 2016; Yavnov, Rakov, 2002]. In river estuaries of Sakhalin Island and the Far East as a whole, this species inhabits sites with a wide salinity range, from almost 0 (nearly freshwater) to 18 psu [Watercourses of Sakhalin Island, 2015; Yavnov, Rakov, 2002]. In the Susuya River estuary, *Corbicula* is characterized by the first type of salinity distribution: in the middle estuary oligohaline zone.

At sta. 44, in the middle estuary oligohaline zone near the shore, the dominance of the Far Eastern brook lamprey *Lethenteron reissneri* (Dybowski, 1869) was recorded. This community, a local one, is typical of the oligohaline part of the estuaries on Sakhalin Island [Labay et al., 2022].

A sharp change in bottom communities is observed in the δ -chorohaline zone, on transect 9. There, two communities with a predominance of chironomids and oligochaetes are localized. The main community is *Chironomus dorsalis* Meigen, 1818 + *Sergentia baueri* Wulker, Kiknadze & Kerkis, 1999 + *Glyptotendipes cauliginellus* (Kieffer, 1913). It occupies most of the reach, from the water's edge to a depth of 1.6 m; it inhabits detritus and siltstone at the river flow speed of $0.01 \text{ m}\cdot\text{s}^{-1}$ and lower at the time of survey. In contrast to the above-described communities, where molluscs, polychaetes, and decapods

played the main role, there, dipterans prevail (see Table 1). With the proportion of dominant chironomids of 86.2% of the total biomass, this community has a short list of subdominants (3 species; 10.3% of the total biomass). Those are an oligochaete *Limnodrilus hoffmeisteri* f. *typica* Claparede, 1862 and chironomids *Trissopelopia longimana* (Staeger, 1839) and *Paratendipes albimanus* (Meigen, 1804). The second community, *Limnodrilus hoffmeisteri* + *Stictochironomus pictulus* (Meigen, 1830) + *Sergentia baueri*, was recorded in the waterway at a depth of 1.3 m on siltstone with detritus. There, the role of oligochaetes increased to 37.7% of the total biomass, and the proportion of chironomids was 54.9%. The contribution of dominant species to the total biomass was 77.5%. Three subdominant species accounted for 22.3% of the integral biomass: chironomids *Gl. cauliginellus* and *P. albimanus*, as well as a polychaete *H. japonica*. Common characteristics of benthic communities of the transitional δ -chorohaline zone are high density (more than 2,000 ind. $\cdot$ m⁻²) with low biomass (several g $\cdot$ m⁻²) and polydominance (three dominant species in each community).

A benthic community uncommon for the lower littoral of Sakhalin Island, with predominance of juveniles of the Japanese mitten crab *Eriocheir japonica* (De Haan, 1835), was recorded at all stations on the riffle separating the Susuya River estuary from above (see Table 1). The community is temporary, and this is due to the life cycle of the dominant species. In Primorye, *Er. japonica* reproduction occurs in brackish water of estuaries at salinity of 5 to 27 psu in May–August; development of planktonic larvae and settling of fry on the bottom is registered during the same period in the adjacent coastal area; and upriver migration of juveniles is in August–October [Kolpakov, Semenkova, 2012]. Therefore, the concentration of juveniles at the first riffle downstream of the Susuya River fits into the life cycle of the Japanese mitten crab. With the onset of winter, the grown crabs leave the riffle, and this leads to a shift in bottom communities.

The *Eriocheir japonica* community is likely to be recorded at the riffle in late summer and early autumn. The density is formed, the same as downstream, mostly by oligochaetes and dipterans (49.7 and 45.6%, respectively), while the biomass basis (91.7%) is formed by decapods represented by one dominant species only. Two subdominant species, an oligochaete *L. hoffmeisteri* and a chironomid *St. pictulus*, account for another 6.4% of the total biomass.

In general, within the Susuya River estuary, five types of benthic communities are identified: the community of the riffle separating the estuary from above (*Eriocheir japonica*); communities of the δ -chorohaline zone (*Chironomus dorsalis* + *Sergentia baueri* + *Glyptotendipes cauliginellus* and *Limnodrilus hoffmeisteri* + *Stictochironomus pictulus* + *Sergentia baueri*); communities of the middle estuary oligohaline zone (*Corbicula japonica*, *Hediste japonica*, and *Lethenteron reissneri*); communities of the lower estuary polyhaline–mesohaline zone (*Fluviocingula nipponica* + *Macoma balthica* and *Macoma balthica*); and the community of the river mouth (*Hemigrapsus takanoi*). The water's edge community (*Eogammarus tiuschovi* + *Hediste japonica*) is confined to the river mouth and the polyhaline zone. The type and location of communities within the estuary are mediated by the salinity regime and the sediment type (the latter is for communities of the upper estuary freshwater zone).

High values of the diversity index by density were observed in communities confined to the mouth and polyhaline–mesohaline and oligohaline zones (1.72–2.20 bit $\cdot$ species⁻¹). In communities located upstream, in the δ -chorohalinity zone, at salinity of 0.08 to 1.6 psu, a significant decrease in I_N was revealed, down to 1.32–1.46 bit $\cdot$ species⁻¹. This phenomenon is governed by the fact as follows. In communities of the δ -chorohaline zone, the entropy principle with a uniform distribution of the indicator by species is violated. Accordingly, a pronounced structuring by density occurs within the community, when 62–92% fall on 1–3 dominant species.

High values of the diversity index by biomass were recorded for polydominant communities (*Eogammarus tiuschovi* + *Hediste japonica*, *Fluviocingula nipponica* + *Macoma balthica*, *Chironomus dorsalis* + *Sergentia baueri* + *Glyptotendipes cauliginellus*, and *Limnodrilus hoffmeisteri* + *Stictochironomus pictulus* + *Sergentia baueri*) and for communities with a low relative biomass of the dominant species (*Hediste japonica* and the unnamed community). Those seem to be localized in areas transitional to the cores of zones identified by salinity.

The ABC index showed several peaks that fell on communities with dominance of large-sized species, regardless of salinity: *Hemigrapsus takanoi*, *Macoma balthica*, *Corbicula japonica*, and *Lethenteron reissneri* (19–33.2%). In fact, the ABC index marks typical estuary communities corresponding to the cores of the mouth and polyhaline–mesohaline and oligohaline zones. The dynamics of the diversity index by biomass is in antiphase to the dynamics of the ABC index.

Using the ordination analysis according to the principal component method for the station-by-station structure of macrobenthos in the area of action of three main independent factors (together, those account for 58.9% of the variance), four main units of stations were identified (Fig. 3). The compact unit combining sta. 29–33, 35, 38–40, 42, 43, 45, and 46 is characterized by the dominance of a bivalve *C. japonica* and is associated with the above-described community of the same name. The second unit, that of sta. 2, 13, 16, 17, 19, 22–27, includes stations belonging to the *Macoma balthica* community. Sta. 1, 6, 8–12, 14, 15, 18, 20, and 21 are close to a set of stations for the *Fluviocingula nipponica* + *Macoma balthica* community. Remaining stations, where other bottom communities are localized, are concentrated in an area of close-to-zero coordinate values and do not follow the major revealed patterns. The resulting picture confirms the identification of the key benthic communities in the oligohaline, mesohaline, and polyhaline estuary zones affected by varying salinity during tidal phenomena.

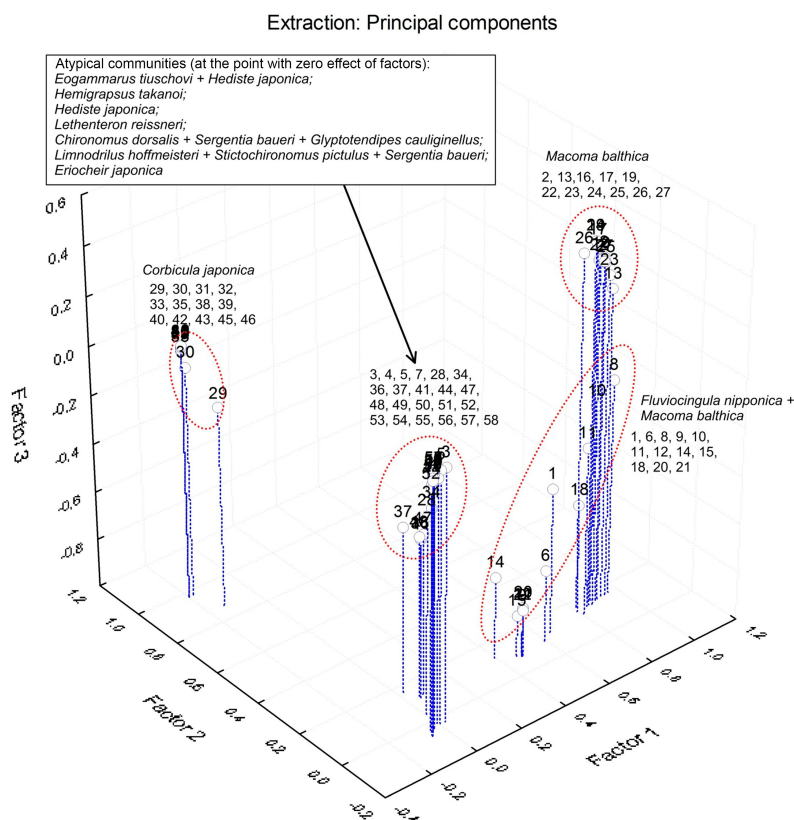


Fig. 3. Principal components analysis (3D ordination) for benthic stations

The correspondence between the distribution of key macrozoobenthic species and the main environmental factors is shown in Fig. 4.

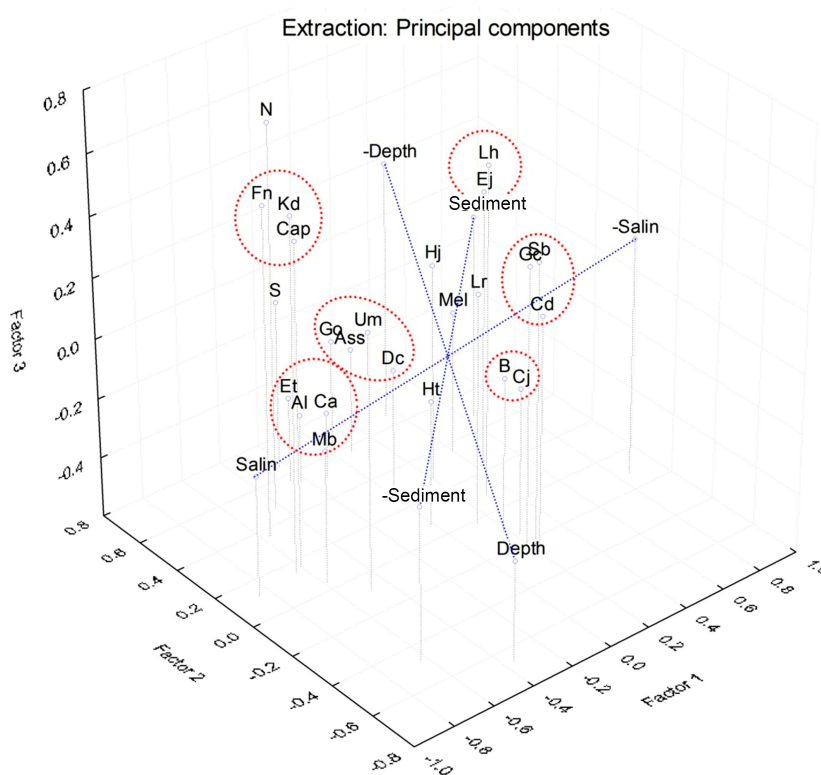


Fig. 4. Principal components analysis (3D ordination) for macrozoobenthic species abundance and biomass and for environmental parameters. Hj, *Hediste japonica*; Cap, Capitellidae; Lh, *Limnodrilus hoffmeisteri*; Fn, *Fluviocingula nipponica*; Ass, *Assiminea lutea*; Mb, *Macoma balthica*; Cj, *Corbicula japonica*; Et, *Eogammarus tiuschovi*; Kd, *Kamaka derzhavini*; Mel, *Melita shimizui* / *Melita* sp.; Al, *Ampithoe lacertosa*; Go, *Gnorimosphaeroma ovatum*; Ej, *Eriocheir japonica*; Ht, *Hemigrapsus takanoi*; Ca, *Cran-gon amurensis*; Dc, *Deiratonotus cristatum*; Um, *Upogebia major*; Cd, *Chironomus dorsalis*; Sb, *Sergentia baueri*; Gc, *Glyptotendipes cauliginellus*; Lr, *Lethenteron reissneri*. Salin, water salinity; depth, depth studied; sediment, sediment type; S, number of species; N, density; B, biomass

For most species, the distribution of the biomass, as might be expected, is determined by the salinity factor. A separate set in the area of its positive effect (a gain in species biomass with increasing salinity values) is formed by species of the polyhaline–mesohaline zone: *M. balthica*, *E. tiuschovi*, *Am. lacertosa*, and *Cr. amurensis* (Figs 5, 6). The second set, also lying on the segment of salinity in the area of its positive effect, unites species abundant in mesohaline and oligohaline waters: *As. lutea*, *Gn. ovatum*, *D. cristatum*, and *Upogebia major* (De Haan, 1841) (see Figs 5, 6). A negative response to an increase in water salinity is demonstrated by chironomids *C. dorsalis*, *S. baueri*, and *Gl. cauliginellus* abundant in the δ-chorohaline zone (see Fig. 6).

Two groups of species are affected by two abiotic factors: salinity and depth. The first group covers Capitellidae polychaetes, a gastropod *F. nipponica*, and an amphipod *Kamaka derzhavini* Gurjanova, 1951, which are common in the river mouth and adjacent areas. This group shows a positive relationship with salinity and a negative one with depth, *i. e.*, the biomass of these species increases with rising salinity and decreasing depth (see Fig. 5). The second group is represented by one species, *C. japonica*, and features the opposite dependance: a negative relationship with salinity and a positive one with depth (see Fig. 5).

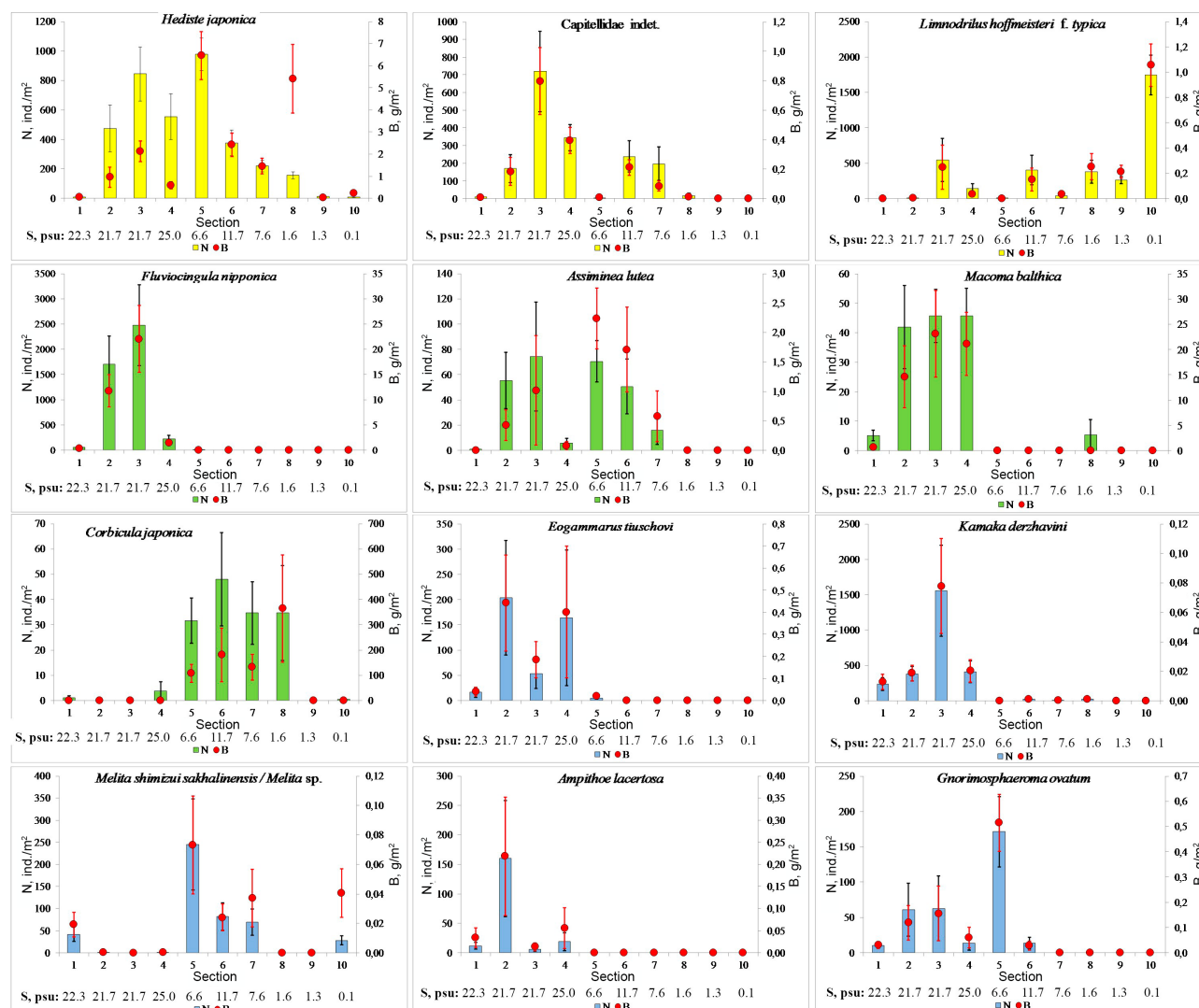


Fig. 5. Distribution of abundant macrozoobenthic species in the Susuya River estuary (Annelida, yellow; Mollusca, green; Amphipoda, blue)

Two species, an oligochaete *L. hoffmeisteri* and a crab *Er. japonica*, are situated far above the area of effect of known environmental factors. Both are abundant in the estuary (see Figs 5, 6). For a crab, such distribution is governed by a biological indicator: the feature of its life cycle.

Other species are located on the 3D plot near the center of the axes (in the area of close-to-zero coordinate values of all three orthogonal factors). Therefore, their distribution in the estuary is subject to other patterns, unknown to us.

Trophic characteristics. Out of 11 trophic groups revealed, only a few form the basis of the biomass on individual transects (Fig. 7). According to the representation of trophic groups, the entire estuary is clearly divided into five areas. The group with a mixed feeding type (detritus feeders, browsers, and scavengers) dominates in macrozoobenthos in the river mouth (94.9% of the total biomass). The biomass is chiefly formed by crabs *H. takanoi* and adult *Er. japonica*, as well as amphipods *E. tiuschovi* and *Eogammarus possjeticus* (Tzvetkova, 1967).

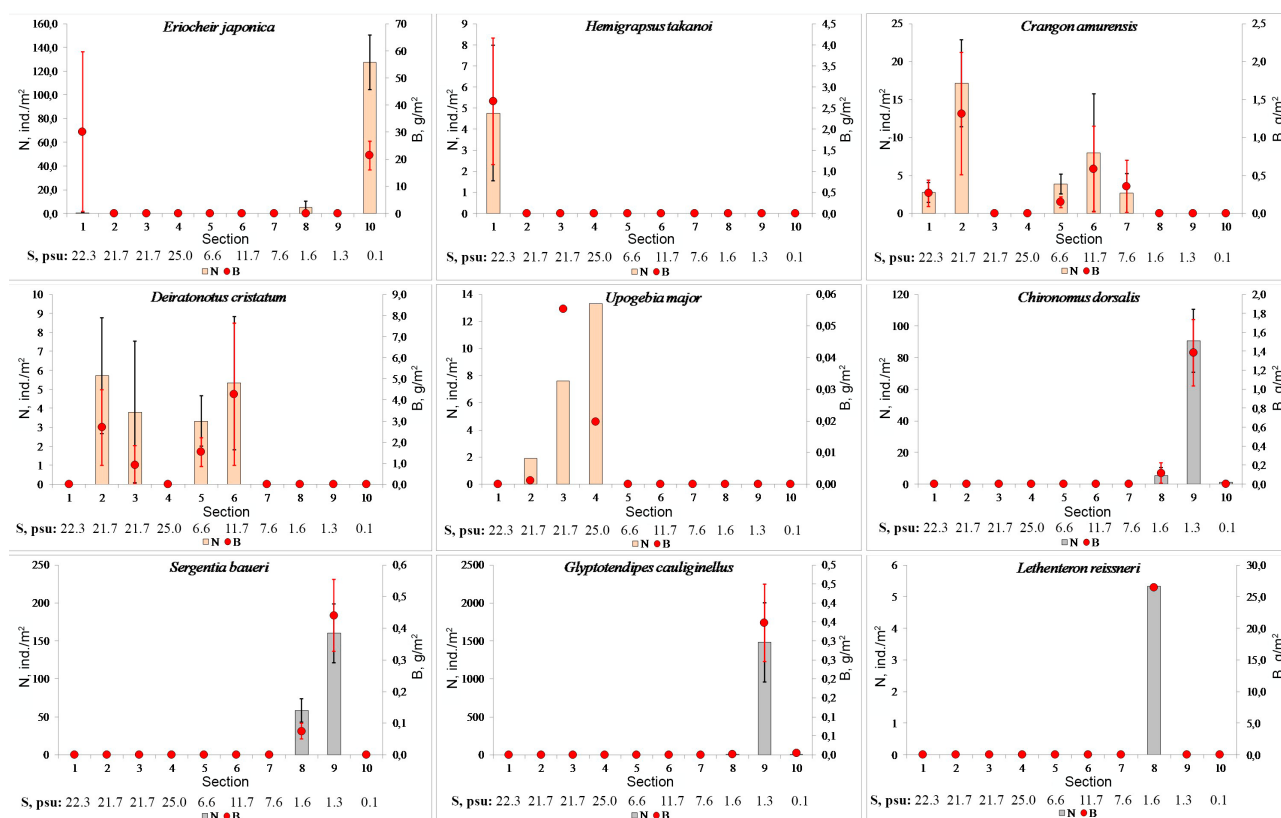


Fig. 6. Distribution of abundant macrozoobenthic species in the Susuya River estuary (Decapoda, light brown; Diptera, grey; Agnatha, grey)

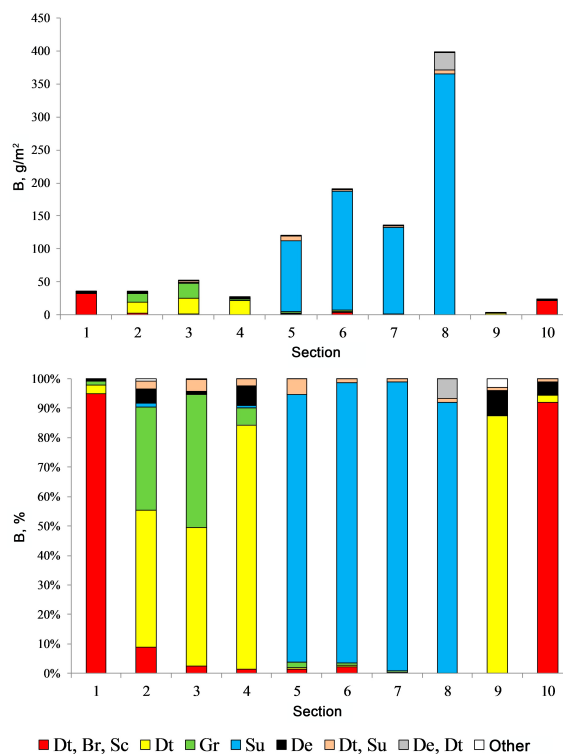


Fig. 7. Spatial distribution of the biomass (B , g·m⁻²) of macrobenthic trophic groups across the Susuya River estuary (abbreviations are explained in the Table 1 note)

For more than 1.5 km from the mouth, on transects 2–4, the most significant trophic groups are detritus feeders (46.6–82.6% of the total biomass) and grazers (5.9–45.1%). The first ones are represented by a bivalve *M. balthica* (41.2–80.7%), Capitellidae polychaetes, a shrimp *Cr. amurensis*, an amphipod *K. derzhavini*, an isopod *Gn. ovatum*, a mysid *N. awatschensis*, etc. The grazers are chiefly epiphytic gastropods *F. nipponica* (5.4–43.1%) and *As. lutea*, an amphipod *Am. lacertosa*, etc.

Between transects 4 and 5, another trophic restructuring of the macrozoobenthos occurs (see Fig. 7). At a distance from the mouth, in 3–7 km, on transects 5–8, the biomass is mainly formed by suspension feeders. The key filter feeder in this area is *C. japonica* (90.8–98.1%). The sharp transition from one feeding type to another corresponds to the 'marginal filter' theory and the mean position of a salinity barrier of 5–9 psu during the warm period [Lisitsyn, 1994]. Upstream of this salinity barrier, a large amount of suspended organic matter is recorded in water; it is consumed by suspension feeders. Below the barrier, after ultrafast sedimentation, deposited organic matter predominates; it is available to detritus feeders.

Above the oligohaline zone, in the δ -chorohalinicum zone, on transect 9, on the reach, the leading role is again played by detritus feeders (87.5% of the total biomass) with a significant contribution of deposit feeders (8.5%). There, the biomass of detritus feeders is formed mostly by chironomids: *Ch. dorsalis*, *S. baueri*, *Gl. cauliginellus*, *P. albimanus*, *St. pictulus*, etc. Deposit feeders are represented by oligochaetes *L. hoffmeisteri* and *Tubifex tubifex* (O. F. Müller, 1773).

In the area of the river riffle separating the estuary from above, the trophic structure of macrozoobenthos is determined by a group with a mixed feeding type: detritus feeders, browsers, and scavengers (92.0% of the total biomass). This group is represented by juveniles of a crab *Er. japonica* (91.7%) and an amphipod *Eogammarus kygi* (Derzhavin, 1923).

All other trophic groups were not significant.

Conclusion. In the Susuya River estuary, five zones are clearly identified by the distribution of the key communities: the mouth zone, lower estuary polyhaline–mesohaline zone, middle estuary oligohaline zone, upper estuary δ -chorohaline zone, and freshwater zone.

The effect of salinity limits the composition of benthic communities. By cluster analysis, 11 macrozoobenthic communities are identified and united into 5 types: the community of the riffle separating the estuary from above (*Eriocheir japonica*); communities of the δ -chorohaline zone (*Chironomus dorsalis* + *Sergentia baueri* + *Glyptotendipes cauliginellus* and *Limnodrilus hoffmeisteri* + *Stictochironomus pictulus* + *Sergentia baueri*); communities of the middle estuary oligohaline zone (*Corbicula japonica*, *Hediste japonica*, and *Lethenteron reissneri*); communities of the lower estuary polyhaline–mesohaline zone (*Fluviocingula nipponica* + *Macoma balthica* and *Macoma balthica*); and the community of the river mouth (*Hemigrapsus takanoi*). The water's edge community *Eogammarus tiuschovi* + *Hediste japonica* is confined to the river mouth and the polyhaline–mesohaline zone. By the methods of ordination analysis, the communities *Corbicula japonica*, *Macoma balthica*, and *Fluviocingula nipponica* + *Macoma balthica* are identified as the key ones of the estuary.

The major environmental factors affecting the distribution of key macrozoobenthic species are water salinity and, to a lesser extent, depth. The type of sediment is not a determining factor in the area of the effect of salinity.

The estuary is clearly divided into 5 zones by the results of the distribution analysis of the trophic groups of macrobenthos as well. The basis of the macrozoobenthic biomass in the river mouth is formed by a group with a mixed feeding type: detritus feeders, browsers, and scavengers. In the lower

estuary zone, the most significant trophic groups are detritus feeders and grazers. Suspension feeders determine the trophic structure of the middle estuary oligohaline zone. In the δ -chorohalinicum zone, the leading role is again played by detritus feeders with a noticeable contribution of deposit feeders. On the river riffle, the basis of the macrobenthic biomass is formed by a group with a mixed feeding type: detritus feeders, browsers, and scavengers; it is represented by juvenile crabs and amphipods.

The study was not sponsored.

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МАКРОЗООБЕНТОС ЭСТУАРИЯ РЕКИ СУСУЯ (ОСТРОВ САХАЛИН): II. ДОННЫЕ СООБЩЕСТВА И РАСПРЕДЕЛЕНИЕ КЛЮЧЕВЫХ ВИДОВ

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Сообщества макрозообентоса и их характеристики в эстуариях рек острова Сахалин изучены недостаточно. В большинстве коротких рек Сахалина состав донных сообществ сильно ограничен по сравнению с таковым эстуариев других рек Дальнего Востока России. В сентябре 2022 г. обследован эстуарий реки Сусуя — полноразмерный по сравнению с эстуариями малых рек

острова. Цель работы — описать основные закономерности распределения донных сообществ, их структуры, ключевых видов и трофических характеристик макрозообентоса вдоль градиента солёности в полноразмерной эстуарии реки Сусуя на острове Сахалин. Методами кластерного и ординационного анализа выделены донные сообщества эстуария. Описаны основные сообщества и трофическая характеристика, особенности распределения ключевых видов макрозообентоса вдоль русла эстуария реки Сусуя. Приведены главные закономерности распределения сообществ макрозообентоса, ключевых видов и трофических группировок в эстуарии реки Сусуя. Выделены 11 сообществ макрозообентоса, объединённых в пять типов: сообщество переката, ограничивающего эстуарий сверху, сообщества δ -хорогалинной зоны, сообщества среднеэстуарной олигогалинной зоны, сообщества нижеэстуарной полигалинно-мезогалинной зоны и сообщество устья реки. Сообщество уреза воды локализовано в устье реки и полигалинно-мезогалинной зоне. Основные сообщества эстуария реки Сусуя — *Corbicula japonica*, *Macoma balthica* и *Fluviocingula nipponica* + *Macoma balthica*. Основными факторами среды, влияющими на распределение ключевых видов макрозообентоса, являются солёность воды и — в меньшей степени — глубина. Тип грунта не выступает как определяющий фактор.

Ключевые слова: эстуарий, макрозообентос, донное сообщество, трофическая характеристика, остров Сахалин